Security areas for maintaining elk on publicly accessible lands during archery and rifle hunting seasons in southwestern Montana



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Executive Summary

Fall elk habitat management on public lands has focused on providing security areas that allow for reasonable elk survival and hunter opportunity. The management focus of maintaining or improving security areas, combined with conservative harvest regulations, may explain why some elk populations have increased in the western United States. However, in areas that include both publicly accessible and inaccessible lands, elk may alter their space use patterns during the hunting season by increasing use of areas that restrict public hunting access rather than utilizing security areas on adjacent public lands. We used GPS location data from 325 adult female elk in 9 populations to determine resource selection during the archery and rifle hunting seasons in southwest Montana. We found that for the covariates over which managers have some control, in order of the strength of selection, elk selected for areas that were not known to be publically accessible for hunting, had higher time-integrated NDVI, higher canopy cover, were further from motorized routes, and had lower hunter effort during the archery season. During the rifle season, in order of the strength of selection, elk selected for areas that were not known to be publically accessible for hunting, further from motorized routes, had higher canopy cover, and higher hunter effort. Interactions among several of these influential covariates revealed dependencies in elk resource selection patterns. Further, cross-population analyses revealed increased elk avoidance of motorized routes with increasing hunter effort during the both hunting seasons. In order to create security areas on public lands during archery season, we recommend managing for areas with $\ge 13\%$ canopy cover that are $\ge 2,760$ m from motorized routes, and identifying and managing for areas of high nutritional resources within these areas. During the rifle season, we recommend managing for areas with $\geq 9\%$ canopy cover that are $\geq 1,535$ m from motorized

routes, and are at least 5,000 acres. Lastly, given increased elk avoidance of motorized routes with higher hunter effort, we recommend that to maintain elk on public lands managers consider increasing the amount of security habitat in areas that receive high hunter effort, or hunting seasons that limit hunter effort in areas of high motorized route densities.

Background

In 2013, biologists from the United States Forest Service (USFS) and Montana Fish, Wildlife and Parks (MFWP) developed collaborative recommendations for elk habitat management on the Custer, Gallatin, Helena, and Lewis and Clark National Forests and identified the need to better understand fall elk distributions and resource selection (MFWP and USFS 2013). Many of the Forest Plans in this area are in the process of being revised, so there is an important opportunity to provide science-based recommendations for formulating standards and guidelines for elk habitat management into the future. MFWP elk population management focuses on maintaining numbers above population viability thresholds, protecting certain sex and age classes from over-harvest, providing public hunting opportunity, and attempting to balance elk distribution across public and private lands. The USFS strives to complement MFWP's efforts through management of elk habitat on USFS lands (MFWP and USFS 2013). As such, both agencies share the management goal of maintaining elk on public lands and work together to design habitat management recommendations to achieve this goal.

Historically, forest management focused primarily on road building and timber management. The cooperative elk-logging studies of the 1970s and 1980s provided some of the first insights into the effects of these activities on elk distributions and developed the concept of managing public lands to include secure areas for elk (Lyon et al. 1985). While specific recommendations were not made, it was recognized that logging activity and the associated roads caused displacement of elk from areas of traditional elk use. Thus, it was recommended that timber harvests should be designed to minimize the number of routes and the duration of logging activity (Lyon et al. 1985).

In the early 1990's, biologists from both agencies recognized that a new management paradigm was needed, leading to the Elk Vulnerability Symposium in Bozeman, Montana in April 1991, hosted by the Montana Chapter of the Wildlife Society. It was here that the concept of security areas for elk was first formalized (Hillis et al. 1991). Hillis et al. (1991) analyzed data collected from radio-collared elk (bulls and cows) during the rifle hunting season in relatively continuous conifer forests in western Montana (Lyon and Canfield 1991). They recommended managing for at least 30% of a valid analysis area in forest blocks of similar canopy cover structure, which were at least 250 acres in size, and at least 0.5 mile from the nearest motorized route. The objective of managing for security areas was to provide reasonable levels of bull elk survival and hunter opportunity during the rifle hunting season. The authors cautioned that the numerical parameters they reported for block size and distance to the nearest motorized route should not be considered an exact 'recipe' to be followed in all situations, but that the concepts (size, distance, and percent of a valid analysis area) could be tailored to an area based on local knowledge. As such, a variety of security definitions, some including specific requirements for minimum forest cover, have been used in developing travel management plans and for evaluating project level effects on elk (Christensen et al. 1993). In areas where forest cover is less contiguous than western Montana, where the Hillis paradigm was generated, the importance of forest cover for security areas has been questioned, but not formally examined.

Extrapolations of Hillis et al. (1991) security area parameters to less densely forested habitats, mixed ownership regions, archery hunting seasons, and female elk survivorship may not be valid, and therefore may not be useful to managers in some areas. In areas that include a matrix of publicly accessible and inaccessible lands, elk may decrease their use of security areas on public lands and increase their use of areas that restrict public hunter access during the hunting season (Burcham et al. 1999, Conner et al. 2001, Hayes et al. 2002, Proffitt et al. 2010, 2013). Additionally, in many areas, hunting seasons are designed to decrease the number of elk, and as such are focused on increasing the harvest of adult female elk rather than providing for bull elk survival. However, if female elk are not available to public hunters in sufficient numbers due to a distribution shift from publicly accessible to inaccessible lands, then harvest is not an effective tool to reduce adult female survival and overall elk population growth. Elk distribution shifts from publicly accessible to inaccessible lands, whether the result of short-term changes in hunting pressure (Millspaugh et al. 2000, Proffitt et al. 2010) or long-term behavioral adaptations (Boyce 1991), is a major challenge to wildlife and land managers as they attempt to maintain elk populations at socially acceptable levels while also meeting public demand for hunting opportunities (Haggerty and Travis 2006).

The timing and degree of changes in elk distributions during hunting season are not consistent across populations, with some populations showing little to no change in distribution across publicly accessible and inaccessible lands during the hunting season, or even increasing use of publicly accessible areas during the hunting seasons (Figure 1). This may be the result of a functional response in resource selection (Mysterud and Ims 1998, Mabille et al. 2012), where the strength of selection for or against a particular resource is dependent on the availability of that resource. Each elk population's annual range is comprised of different proportions of publicly accessible lands with different levels of hunter pressure. Thus, differences in the strength of selection for or against various habitat attributes may be related to these differences in hunter access and hunter pressure (e.g., elk may respond more strongly to motorized routes in areas with greater hunter pressure). Additionally, the effects of the archery and rifle season on elk distributions vary across populations and likely correlate with different degrees of hunting pressure. Some elk populations begin redistribution during the archery season (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2013), whereas others do not respond until during the rifle season (Millspaugh et al. 2000, Johnson et al. 2004, Proffitt et al. 2013), if at all. Differences in hunter pressure during rifle and archery seasons, as well as differences in topography and elk migratory behavior have been suggested to explain the differences in selection among populations (Conner et al. 2001, Proffitt et al. 2013), and better understanding of these differences in selection is a priority identified in the collaborative elk habitat management recommendations (MFWP and USFS 2013).

While most research and management has focused on the impacts of rifle hunting on elk, archery hunting has been increasing in popularity, with a 98% increase in archery license sales in Montana since 1985 (Montana Fish, Wildlife and Parks, unpublished data). As such, it is important to examine elk responses to archery hunting. Archery hunting has the potential to lead to reduced pregnancy rates and delayed conception in elk (Davidson et al. 2012). Nutritional condition of female elk during the late-summer and rut is also related to pregnancy rates and conception (Noyes et al. 2004, Cook et al. 2013). It is therefore possible that human disturbance associated with archery hunting may shift elk distributions away from areas of high nutritional resources, potentially impacting elk population dynamics further than would be expected through archery hunting mortality alone.

Here, we used fine-scale location data collected during 2005–2014 to assess female elk resource selection during the archery and rifle hunting seasons in 9 elk herds in southwestern Montana. We also examined potential functional responses in elk resource selection by comparing the standardized coefficient estimates from population-specific models along gradients of accessible:inaccessible lands and mean hunter pressure to determine if the relative availability of publicly accessible land or population-specific hunter pressure influence the direction and/or strength of elk resource selection during the hunting seasons. Finally, we evaluated the traditional paradigm of elk security areas (Hillis et al. 1991) against security area metrics derived from our top resource selection function models for archery and rifle hunting seasons.

Methods

Study Area

The study area included the annual ranges of 9 elk populations in southwestern Montana (Figure 2). Climate in these ranges is characterized by short, cool summers and long, cold winters. Vegetation types across these ranges included a mix of montane forest (e.g., aspen [Populus tremuloides], Douglas fir [Pseudotsuga menziesii], lodgepole pine [Pinus contorta]), open sage-grassland (e.g., big sagebrush [Artemesia tridentata], blue-bunch wheatgrass [Pseudoroegneria spicata], Idaho fescue [Festuca idahoensis]), and upland grasslands, meadows, and unvegetated areas, but the relative proportions of these habitat types varied among the populations. All elk ranges included a mix of public lands that are generally accessible to public hunters, primarily managed by the United States Forest Service or Bureau of Land Management, privately owned lands that are accessible to hunters through a State of Montana hunter access program, and privately owned lands with unknown but likely varying degrees of restrictions on public hunting access. Elevation, motorized route densities, and indices of nutritional resources varied among the populations' ranges (Table 1). Mule deer (Odocoileus hemionus), white tail deer (Odocoileus virginianus), bighorn sheep (Ovis canadensis), and moose (Alces alces) also occupy the elk ranges. Wolves (Canis lupus), mountain lions (Puma concolour), black bears (Ursus americanus), and coyotes (Canis latrans) are the elk predators in the system, and grizzly bears (*Ursus arctos*) are also found in the ranges in the eastern portion of the study area. For full descriptions of the elk habitats for these populations, see Gude et al. (2006), White et al. (2012), Proffitt et al. (2013, 2014).

Data Collection

During 2005–2014, we captured and radiocollared adult female elk from 9 populations in southwestern Montana on their winter ranges using helicopter net-gunning or chemical immobilization. Elk populations were selected for capture and radiocollaring as part of several different projects related to carnivore-elk interactions, elk brucellosis, or elk survival investigations. Collar functionality differed among populations and years, and all collars contained GPS receivers that collected 12–48 locations per day for a minimum of 1-year. Because our goal in this project was to synthesize data collected across a large spatial scale, we pooled data from these 9 elk populations to create a regional elk location dataset, as well as used the individual population datasets.

Data Analysis

We developed separate archery- and rifle-season resource selection functions using a used-available framework (Johnson 1980, Manly et al. 2007). Archery and rifle seasons for each

year were defined by the Montana Fish, Wildlife, and Parks hunting season dates (Appendix S1). We treated locations collected from the GPS collars as the used sample. We randomly selected 4 locations per individual per day to reduce spatial autocorrelation in the data (Hansteen et al. 1997). In order to maintain equal sampling effort for all individuals, we only used data from the first year each individual was collared. We defined population-specific annual ranges by randomly selecting 1 location per day per individual to reduce spatial autocorrelation among the locations, and then building 99% kernel density estimator (KDE) contours. We randomly generated available points at a 1:5 used:available ratio within the population-specific annual range (Northrup et al. 2013).

We evaluated 9 covariates describing elk resource selection based on a review of previous elk studies and current metrics used for elk habitat management (Lyon 1979, Hillis et al. 1991, Christensen et al. 1993, Pettorelli et al. 2011, Proffitt et al. 2011, McCorquodale 2013, Ranglack et al. In Review). To represent roads and other motorized routes, we included distance to motorized routes. In this case, only routes that were open to public motorized use during the hunting season were included. All other routes (private, administrative or closed routes) were excluded. To represent general landscape characteristics, we included 4 landscape attributes: canopy cover, slope, elevation and solar radiation. Hunting pressure was represented using 2 covariates: accessible for public hunting (hunter access) and hunter effort. Hunter access was a binary covariate contrasting lands that were freely and publically accessible with private lands with some level of restriction to public access. For this analysis, public lands that permitted hunting and private lands enrolled in the State of Montana's Block Management hunter access program were considered publicly accessible, and all other lands were considered lands that may have restricted public hunter access. Hunter effort was estimated annually per hunting district using the Montana Fish, Wildlife and Parks harvest survey program, and we created an index of hunter pressure for each hunting district as hunter days/km² (based on the area of the whole hunting district regardless of hunter access), which we used for both the archery and rifle seasons. During the archery season (Appendix S1), we included a remotely sensed metric of greenness derived from the Normalized Difference Vegetation Index (NDVI), time integrated NDVI, to represent effects of nutritional resources on selection. Time integrated NDVI represents the net primary production during the growing season (Jonsson and Eklundh 2002, White et al. 2009), and is an important factor influencing summer elk resource selection in this area (Ranglack et al. 2016). During the rifle season we included snow water equivalent (SWE) as a covariate representing effects of snowpack on selection. We generated SWE values based on the max SWE value from SNOWDAS (National Operational Hydrologic Remote Sensing Center 2004) for each pixel during each of six 6-day periods during the rifle season which we called 'hunt period'. These hunt periods were unique for each year. Full details on covariate development are included in Appendix S2.

Although resource selection analyses are typically conducted at the resolution of the available covariate data, animals may perceive and select resource attributes at different spatial scales (Anderson et al. 2005, Laforge et al. 2015, DeVoe et al. 2015), therefore, we considered each continuous covariate over 6 different spatial scales (30, 100, 250, 500, 750, 1000 m; Table 2). Additionally, because the relationship between selection and covariates might be nonlinear, we evaluated multiple functional forms (linear, quadratic, pseudothreshold) for each continuous covariate. This allowed us to fit either straight lines or curves to the data, depending on which received more support. We evaluated spatial scale and functional forms for each covariate in an

exploratory analysis, unless the most appropriate functional form could be identified *a priori* from existing literature (Table 2).

We screened all continuous covariates for multi-collinearity using Pearson correlation coefficients. Any covariates that were found to be collinear ($r \ge |0.7|$) with one another were not included in the same model. First, we examined all possible univariate models in an exploratory analysis to determine the most explanatory functional form(s) and spatial scale(s) for each covariate. We considered covariates from all the models within 5 AIC_c units of the top model and advanced only these covariates to the next step. Then, we combined the top covariate forms and scales in all possible combinations to determine the overall best-supported model for elk resource selection during the hunting seasons. We also included interactions between hunter access and distance to motorized routes, hunter access and canopy cover, distance to motorized routes and time integrated NDVI/SWE (archery/rifle), and distance to motorized routes and hunter effort. We developed separate models for the archery and rifle seasons.

We pooled data from all herds and fit models using a conditional logistic regression model, conditioned on 'herd-year' (unique for each population by year combination) for the archery season to allow for the annually varying time integrated NDVI values and 'herd-hunt period' (unique for each population and hunt period combination) for the rifle season to allow for the 6-day variation in SWE. We chose this modeling framework to ensure that the available points for each stratum were evaluated against the used points for that stratum, since there were time varying covariates, a different set of instrumented individuals for each year, and different available choice sets for each population.

To determine if the strength of selection for covariates differed across herds with different levels of hunter effort and hunter access, we then fit population-specific models and explored the functional response between the distance to motorized routes, canopy cover, hunter effort, and hunter access standardized coefficient estimates along gradients of accessible:inaccessible lands and hunter pressure, as these varied among populations. Population-specific models were fit using the same model structure as that found in the top pooled model. As our dependent variables (standardized model coefficient estimates) were estimates with associated standard errors instead of measured values, each estimate was weighted by the inverse of the variance (Marin-Martinez and Sanchez-Meca 2009), such that estimates that were estimated with greater precision were given more weight than those that were estimated with less precision. We identified functional responses as significant if the 95% confidence intervals on the slope of the estimated regression lines did not overlap 0.

To compare results of our top models with the traditional security area paradigm, we evaluated the relative support from the data for our resulting top models and models representing the traditional security area paradigm (Hillis et al. 1991, Christensen et al. 1993). To do so, we examined plots from our top models depicting how relative resource selection changes as canopy cover and distance to motorized routes increase across the range of available values for publicly accessible elk during each season while holding all other covariates at their means. From those, we identified the values of canopy cover and distance to motorized routes where relative resource selection begins to reach a pseudothreshold, which we arbitrarily defined as having a relative slope of 0.5 (slope = range of Y values/(2 * range of X values)). These cutoff values were considered to be analagous to the dense forest canopy cover (e.g. \geq 40%) and \geq 0.5 mile distance to motorized route thresholds commonly used in the traditional security area paradigm (Hillis et al. 1991, Christensen et al. 1993). To test the influence of block size on elk selection of

areas with canopy cover and distance from motorized routes attributes considered indicative of security areas, we varied the block size of our security area definitions to include areas ≥ 0 acres (no size requirement), 250 acres, ≥ 500 acres, $\geq 1,000$ acres, $\geq 2,000$ acres, and $\geq 5,000$ acres. To determine the importance of the canopy cover component of traditional security areas, we evaluated models representing traditional security areas with a range of canopy cover values (≥ 0 , 10, 20, 30, 40, 50, 60, 70%), while holding the distance to route (≥ 0.5 miles) and size of the block (≥ 250 acres) constant.

To compare traditional security areas with those identified in our analyses, we extracted values for both used and available points from our new security metrics and the traditional paradigm with varying canopy cover metrics. We then fit our top model for each season, replacing the canopy cover and distance to motorized routes covariates with either the traditional security area paradigm with varying canopy cover or our new security area values. This resulted in a total of 8 traditional security area metrics and 6 security area metrics derived from our analyses for each season. We compared these models using AIC $_c$ to determine which combination of canopy cover, distance to motorized routes, and block size covariates was most supported by the data, where models with ΔAIC_c values from 0-2 were considered equally supported, 2-10 showed less support, and values >10 were not supported.

Lastly, to determine if the proportion of security areas within a population home range influenced the extent to which the population redistributed from publicly accessible to inaccessible lands through the course of the fall hunting seasons, we examined a potential relationship between elk redistribution and the proportion of the annual range qualified as a security area, using linear regression. We quantified redistribution as the difference between the proportion of used locations on publicly accessible lands in August and the proportion of used locations on publicly accessible lands during the rifle season for each population. The proportion of the population annual range defined as a security area was based only on the publicly accessible portion of the annual range, and was calculated based on the security area metrics from our top archery and rifle models, as well as using the Hillis et al. (1991) security area definition.

Results

We used a total of 57,282 archery season and 47,602 rifle season elk locations collected from 325 individual elk in our analyses. Of the elk locations, 61.9% and 52.5% occurred on publicly accessible lands during the archery and rifle seasons respectively. Mean elevation of the elk locations was 6,903 ft (SD = 1,519) and 6,578 ft (SD = 1,378) during the archery and rifle seasons, respectively. Mean distance to motorized routes of the elk locations was 1.61 miles (SD = 1.85) and 1.28 miles (SD = 1.31) during the archery and rifle seasons respectively. Mean time integrated NDVI of the elk locations during the archery season was 52.6 (SD = 11.6). Mean SWE of the elk locations during the rifle season was 1.09 in. (SD = 1.13). The mean slope of the elk locations was 14.3 degrees (SD = 9.4) and 14.1 degrees (SD = 8.9) during the archery and rifle seasons respectively. The mean canopy cover of the elk locations was 27.7% (SD = 25.2) and 19.6% (SD = 23.2) for the archery and rifle seasons respectively. Information on what was available for each population's annual range can be found in table 1.

Archery season elk resource selection

Using the pooled regional dataset, the full archery season model was the most supported model of elk resource selection during the archery hunting season, with the next best model

having a $\Delta AIC_c = 80.4$. In general, elk were more likely to use areas that were not known to be publicly accessible. Regardless of accessibility, elk were less likely to use hunting districts with higher hunter effort. Further, elk were more likely to use areas as distance to motorized routes, canopy cover, time integrated NDVI, and solar radiation increased, though distance to motorized routes and canopy cover quickly reached a psuedothreshold at ≥ 1.71 miles and $\ge 13\%$ respectively for publicly accessible lands, after which further increases in distance to motorized routes and canopy cover resulted in only small increases in elk resource selection. Elk were also more likely to use moderate slopes (Fig. 3, Table 3). All interactions improved model fit. Model results indicated that at high NDVI values, there was little difference in elk selection for areas near versus far from motorized routes, but at low NDVI values, elk were more likely to use areas far from motorized routes. Elk also were less likely to use areas with higher hunter effort if they were closer to motorized routes, but elk showed little response to increases in hunter effort far from motorized routes. Additionally, the difference in strength of selection for areas with high and low canopy cover were greater on publicly accessible lands that on lands that are not known to be publicly accessible. This same pattern was also found for the difference in the strength of selection for areas near and far from motorized routes (Fig. 4, Table 3, Appendix S4).

Rifle season elk resource selection

Using the pooled regional dataset, the full model was the most supported model of elk resource selection during the rifle hunting season, with the next best model having a $\Delta AIC_c =$ 36.6. Similar to the archery hunting season model, elk were more likely to use areas that were not known to be publicly accessible during the rifle season. Regardless of accessibility, elk were more likely to use areas as distance to motorized routes, canopy cover, hunter effort, and solar radiation increased, and less likely to use areas as elevation and SWE increased. Elk responses to distance to motorized routes, canopy cover, and hunter effort quickly reached pseudothresholds at ≥ 0.95 miles, $\geq 9\%$, and ≥ 3.44 hunter days/mile² respectively for publicly accessible lands, after which further increases in distance to motorized routes, canopy cover, and hunter effort resulting in only small increases in elk resource selection. Elk also were more likely to use moderate slopes (Fig. 5, Table 3). All of the interactions improved model fit. Elk showed a stronger response to increases in SWE when far from motorized routes than when near motorized routes. Elk showed stronger selection for areas further from motorized routes as hunter effort increased, while they showed little response to increases in hunter effort when near motorized routes. Similar to the archery season, the difference in strength of selection for areas with high and low canopy cover were greater on publicly accessible lands than on lands that are not known to be publicly accessible. However, contrary to the archery season results, the difference in the strength of selection for areas near and far from motorized routes was greater in areas not publicly accessible (Fig. 6, Table 3, Appendix S4).

Functional Response

We detected no changes in the strength of selection for areas that had higher canopy cover, were not publicly accessible, or had lower hunter effort with increases in the ratio of accessible:inaccessible lands and hunter effort during the archery and rifle seasons (Table 4, Appendix S3). However, elk were significantly ($p \le 0.05$) more likely to use areas further from motorized routes as mean hunter effort in the annual range increased during both the archery (Fig. 7a) and rifle seasons (Fig. 7b). This response was very similar during the rifle season and the archery season (Table 4).

Security Areas

Based on the top model from the archery season, we identified areas with $\geq 13\%$ canopy cover (1,000 m spatial scale) and ≥ 1.71 miles from a motorized route as security areas for elk during the archery season. The model including these two parameters, without a defined minimum block size (≥ 0 acres), received the most support, with the next best model having a $\Delta AIC_c = 88.9$ (Table 5). All of the new security area metrics arising from our most supported archery season model were more strongly supported than all of the traditional security area metrics. Of the traditional security area metrics with a minimum block size of 250 acres at least 0.5 miles from a motorized route, $\geq 10\%$ canopy cover was the most supported (Table 5).

Based on the top model from the rifle season, we identified areas with $\geq 9\%$ canopy cover (1,000 m spatial scale) and ≥ 0.95 miles from a motorized route as security areas for elk during the rifle season. The model including these two parameters with a minimum block sizes of 5,000 acres received the most support, with the next best model having a $\Delta AIC_c = 24.7$ (Table 5). Again, all of the new security area metrics derived from our most supported rifle season model were more strongly supported than all the traditional security area metrics. Of the traditional security area metrics with a minimum block size of 250 acres at least 0.5 miles from a motorized route, $\geq 0\%$ canopy cover (i.e., no canopy cover threshold) was the most supported (Table 5). Maps comparing the top archery and rifle security metrics with the traditional security area paradigm can be found in Appendix S5.

No relationships were found between the amount of elk redistribution from accessible to inaccessible lands and the proportion of the annual range in any of the security area metrics (Figure 8).

Discussion

Overall, our results suggest that elk habitat management during the hunting seasons should focus on accessibility of lands for public hunting, motorized routes, and canopy cover. These covariates all had significant effects on female elk resource selection during the archery and rifle seasons and are under some degree of management control. Additionally, nutritional resources are important drivers of female elk resource selection during the archery hunting season and should be considered in elk archery hunting season habitat management strategies. Depending on population size objectives (increase or decrease elk population size) managers can attempt to manipulate each of these factors to make elk more or less vulnerable to harvest. However, managers should also consider that increases in hunter effort or motorized routes may encourage elk to select for areas that restrict public hunter access. We also recommend that new security area metrics derived from our most supported models be considered for southwest Montana (Table 5). Because these metrics are predictive of female elk resource selection, they may encourage elk to remain on publicly accessible lands throughout the hunting seasons thereby enabling sufficient harvest to affect population size and providing season long public land hunter opportunities.

Our modeling of elk resource selection during the archery and rifle hunting seasons suggests that, in general, female elk have similar resource selection patterns in both seasons, as suggested in the collaborative elk habitat management recommendations (MFWP and USFS 2013), particularly in relation to covariates over which managers have some level of control (distance to motorized routes, canopy cover, and hunter access). Lands that were not known to be publicly accessible to hunters were preferred to publicly accessible lands during both seasons.

Thus, we recommend that managers work closely with private landowners to increase public hunting opportunity on private lands. Additionally, the results of our functional response analysis suggest that high hunter effort during the archery season increases elk avoidance of areas near motorized routes (Fig. 7a) in a similar manner to elk responses during the rifle season (Fig. 7b). In order to maintain elk distribution on publicly accessible lands, we recommend managers consider wildlife related motorized travel closure dates that include both archery and rifle season in areas of high hunter effort, or hunting seasons that limit hunter effort in areas of high motorized route densities, similar to what was described in the collaborative elk habitat management recommendations (MFWP and USFS 2013).

The increase in elk selection for areas farther from motorized routes with increases in hunter effort (Fig. 7) helps to explain the documented shift in elk movements during archery hunting seasons that occur in some areas (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2013). Contrary to Vieira et al. (2003), who found that hunter effort during the archery season did not influence elk movement to private lands, we found that hunter effort influenced elk resource selection during the archery season, as elk generally avoided areas of high hunter effort, with this response being even stronger in areas near motorized routes. In our study sites, this selection pattern also involves elk selecting for lands not known to be publicly accessible, which had one of the strongest effects on elk resource selection during the archery season. Security for elk on publicly accessible lands has traditionally been regarded as areas away from motorized routes with high canopy cover that can maintain elk even during periods of hunting stress (Lyon 1979, 1983, Hillis et al. 1991). We found that hunter access had a stronger influence on elk resource selection in both hunting seasons than either distance to motorized routes and/or canopy cover (Table 3).

The influence of late-summer nutrition on ungulate population dynamics and resource selection has been well documented (Cook et al. 2004, 2013, Monteith et al. 2014, Ranglack et al. In Review), but the potential effects of nutrition on archery season elk distributions have not been previously evaluated. Using data from these same study areas, Ranglack et al. (In Review) found that during July and August, female elk were much more likely to be found in areas of high nutritional resources (as represented by time-integrated NDVI). Additionally, motorized routes had a relatively small influence on female elk resource selection during July and August (Ranglack et al. In Review). Using standardized coefficient estimates to compare summer and archery season effects in the same 9 elk herds, female elk avoidance of motorized routes nearly doubles during the archery season, while selection for areas with higher time integrated NDVI values decreased by nearly half. Our results suggest that during the archery hunting season, female elk still seek out areas of high nutritional value even when they are near motorized routes (Figure 4), but this selection for areas of high nutritional value has been reduced, likely due to the increased avoidance of motorized routes or selection for the other covariates that we documented as influential. If elk are attempting to select for areas of high nutritional value throughout the archery hunting season but are unable to do so due to other influences on archery season resource selection, archery hunter pressure may affect elk access to these areas of high nutritional value, and therefore compromise nutritional status at a critical time of year (Noyes et al. 2004, Davidson et al. 2012). This suggests that archery hunting has the potential to affect fall nutritional condition of female elk, and potentially pregnancy rates and body fat levels of elk entering the winter season. We recommend that this topic needs more investigation, and that managers may need to consider including motorized route closures, earlier closure dates during travel planning, and limits on hunter numbers during the archery season in areas of high

nutritional value for elk if maintaining elk access to nutritional resources is part of the management intention. Additional work is also needed to better understand the relationship between NDVI and forage plant communities, and provide recommendations for vegetation management aimed at quantifying and/or improving elk nutritional resources.

During the rifle season, similar to the archery season, elk avoided areas near motorized routes. This response was stronger than during the archery season, indicating that the impact of motorized routes on elk resource selection continues to increase from summer (Ranglack et al. In Review) to archery to rifle seasons. While not unexpected given the vast literature on road effects on ungulates (see McCorquodale 2013 for review), these differences suggest that elk response to motorized routes varies seasonally and is strongly related to the risks associated with hunting seasons. We identified different thresholds in our most supported models; during the archery season we found that elk selected for areas ≥ 1.71 miles from the nearest motorized route, while this distance decreases during the rifle season to ≥ 0.95 miles. This may indicate that while the overall influence of motorized routes on elk resource selection during the archery season is lower than during the rifle season, the spatial scale of effects during archery season is larger. This may be because archery hunters are more apt to hike further away from motorized routes in pursuit of elk. In contrast, rifle hunters have a stronger, but more limited area of influence around motorized routes. The impact of motorized routes on elk resource selection during the hunting seasons is further supported by the functional response depicting increasing selection for areas further from motorized routes with higher hunter effort (Figure 7). Given the increasing popularity of archery hunting, the different impacts of archery and rifle hunters should be incorporated into management designed to maintain elk on public lands by extending motorized route closures such that they include the archery season, as suggested in the collaborative elk habitat management recommendations (MFWP and USFS 2013). Additionally, due to the larger spatial influence of motorized routes during the archery season, some motorized routes may warrant closure during the archery season only and can be re-opened during the rifle hunting season. These archery only closures could be used to protect nutritionally valuable areas.

The traditional security paradigm of managing for blocks of unfragmented forest cover away from motorized routes (Lyon 1979, 1983, Hillis et al. 1991) has been widely accepted. Our results suggest that similar security paradigms could be applied to southwestern Montana in efforts to encourage female elk to utilize public lands. During the archery season, our analysis suggests that areas with $\ge 13\%$ canopy cover (1,000 m scale) that are ≥ 1.71 miles from the nearest motorized route may be perceived by female elk as secure, regardless of block size. During the rifle season, areas with $\geq 9\%$ canopy cover, that are ≥ 0.95 miles from the nearest motorized route, with a block size of \geq 5,000 acres may be perceived by female elk as secure. This, along with our analysis of the traditional paradigm with varying levels of canopy cover (Table 5), suggests that the often used 40% canopy cover threshold for security areas is too stringent, and that the influence of motorized routes is more important than canopy cover to female elk resource selection, as suggested in the collaborative elk habitat management recommendations (MFWP and USFS 2013). Indeed, our models show that while some level of canopy cover is preferred over open areas, the influence of canopy cover on elk resource selection reaches pseudothresholds at relatively low values for both hunting season (Figures 3 and 5). While having patches of dense forest cover may be valuable for elk as hiding cover in the face of disturbance, security areas need not contain 100% hiding cover (hiding cover proxy is ≥40% canopy cover, MFWP and USFS 2013). We found that for the archery season no minimum block size requirement was supported by our data, while the largest minimum block

size we tested (5,000 acres) was supported during the rifle season. This pattern perhaps reflects the generally higher hunter pressure during the rifle season than the archery season, leading to a need for large security areas.

While it may be beneficial to increase the proportion of security areas within population annual ranges if the goal is to reduce hunting stress on elk, we found no relationship between the proportion of security areas within the annual range and the amount of redistribution that occurs in these elk populations (Figure 8). This highlights that even when security areas are available on publicly accessible lands, elk may still choose to redistribute to lands that are not known to be publicly accessible (MFWP and USFS 2013). This may be due to learned behaviors that are passed from one generation to the next (Boyce 1991), or due to additional security from hunting risk on lands not known to be publicly accessible than is found in security areas on publicly accessible land. In any case, it highlights the importance of wildlife and land management agencies working collaboratively with private landowners in managing elk habitat.

Overall, we saw very similar patterns of resource selection during the archery and rifle hunting seasons in terms of direction of selection for the different covariates. However, the direction of selection for hunter effort changed from the archery to rifle season (Table 3). During the archery season, when elk are not limited by snow and the effect of motorized routes is weaker, elk are more likely to use areas with lower hunter effort. However, during the rifle season, elk are more limited in the habitats that are available to them. Hunters may in turn respond to these more tightly defined elk resource selection patterns, making it appear that elk are more likely to be found in areas of high hunter effort when in reality hunter effort may be higher where elk are more likely to be present.

Finally, our results confirm many of the collaborative elk habitat management recommendations for elk habitat management (MFWP and USFS 2013). Similar to Hillis et al. (1991), we caution users that the numerical guidelines may not be valid in all cases and that strict application of the results should be avoided. Extrapolation of these results beyond the study area may or may not be appropriate as results generated in one area may perform extremely poorly when applied in areas that are geographically distant or dissimilar ecologically (Ranglack et al. In Review). However, managers could use this information as a guide for developing hunting season management strategies directed at both hunters and habitat. We recommend a collaborative management strategy that may include adjustments to both the habitat features described above, as well as overall hunter pressure through changes in hunting season structures and working with private landowners to increase public hunter access.

Recommendations:

- 1) We recommend that current fall elk habitat management based on managing motorized route density and providing security areas for elk during the rifle season (Hillis et al. 1991, Christensen et al. 1993) should be expanded to also include the archery season. We found elk responses to hunting risk during the archery season were similar to elk responses during the rifle season.
- 2) We recommend that managers consider the influence of nutritional resources on elk distributions during the archery season. Managers can use time integrated NDVI as an assessment too to identify areas of optimal nutrition (i.e., values ≥ 66, free access at http://phenology.cr.usgs.gov/get_data_250w.php). This product is available to FWP staff through the FWP mapper system.

- 3) We recommend that managers assess the balance between hunter pressure and motorized routes in their area and consider wildlife related travel closure dates during both archery and rifle hunting season in areas of high hunter pressure (≥12.75 hunter days/mile²), or hunting seasons that limit hunter pressure in areas of high motorized route densities.
- 4) We recommend that managers work closely with private landowners to increase public accessibility on private lands if management goals are to maintain a distribution of elk across both public and private lands throughout the hunting seasons.
- 5) We recommend that security areas be defined as having ≥13% canopy cover that are ≥1.71 miles from a motorized route during the archery season, with no minimum block size requirement, and as having ≥9% canopy cover that are ≥0.95 miles from a motorized route, that are at least 5,000 acres during the rifle season.

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Table 1. The mean and standard deviation (in parentheses where applicable) of landscape attributes and annual precipitation at 9 elk population annual ranges within the southwestern Montana study area.

Population	Elevation (ft)	Distance to Motorized Routes (miles)	Canopy Cover (%)	Time Integrated NDVI	Proportion Publicly Accessible	Hunter Effort (days/mile²)
Bitterroot	6,289	1.03	26.4	48.3	0.77	19.4
East Fork	(1,079)	(1.16)	(25.7)	(11.4)		(10.8)
Bitterroot	6,257	1.24	35.8	45.1	0.96	4.92
West Fork	(899)	(1.37)	(23.4)	(8.8)		(0.60)
Dla al-4a:1	7,218	1.14	14.9	51.0	0.82	12.6
Blacktail	(866)	(1.02)	(22.6)	(13.0)		(6.55)
Dome	7,972	3.96	26.2	53.0	0.19	5.10
Mountain	(925)	(3.37)	(24.1)	(9.6)		(10.8)
Madison	7,457	1.85	26.0	52.1	0.62	15.0
Valley	(1,168)	(1.77)	(25.9)	(12.6)		(7.82)
Paradise	7,198	2.12	25.0	47.3	0.45	21.3
Valley	(1,391)	(1.91)	(24.1)	(11.9)		(8.03)
·	7,034	1.04	25.8	44.8	0.75	15.3
Pioneers	(938)	(0.97)	(28.9)	(13.1)		(6.94)
G G 1	7,142	1.50	10.6	50.4	0.81	10.7
Sage Creek	(741)	(1.38)	(19.7)	(12.9)		(3.55)
G 1.	4,764	0.55	25.2	40.2	0.56	15.1
Sapphires	(1,119)	(0.62)	(25.6)	(12.2)		(3.29)

Notes: The values presented above are based on the minimum spatial scale available for each of the covariates.

Table 2. The covariates included in analysis of female elk archery season and rifle season resource selection in southwest Montana, with the spatial scales (in meters) and the functional forms (linear, pseudothreshold, quadratic) or data type (binary) that were evaluated for each covariate.

Covariate	Functional Form(s)	Spatial Scale(s)	Season(s)
Access	Binary	30 m	Both
Canopy Cover	Pseudothreshold	30, 100, 250, 500, 750, 1000 m	Both
Distance to Motorized Routes	Pseudothreshold	30 m	Both
Elevation	Quadratic	30, 100, 250, 500, 750, 1000 m	Both
Hunter Effort	Linear, Pseudothreshold	Hunting Unit	Both
Slope	Quadratic	30, 100, 250, 500, 750, 1000 m	Both
Snow Water Equivalent	Linear, Pseudothreshold	1000 m	Rifle Only
Solar Radiation	Quadratic	30, 100, 250, 500, 750, 1000 m	Both
Time Integrated NDVI	Pseudothreshold	250, 500, 750, 1000 m	Archery only

Table 3. The functional form, spatial scale, standardized coefficient estimates and 95% confidence intervals (in parentheses) for the top regional model of archery season and rifle season female elk resource selection in southwest Montana.

Covariate	Arcl	nery	Ri	Rifle		
	Functional Form	Coeff. Estimate	Functional Form	Coeff. Estimate		
	and Spatial Scale	(CI)	and Spatial Scale	(CI)		
Access	Binary;	-0.75	Binary;	-0.93		
	30 m	(-0.78, -0.72)	30 m	(-0.96, -0.91)		
Canopy Cover	Pseudothreshold;	0.55	Pseudothreshold;	0.41		
1,0	1,000 m	(0.51, 0.60)	1,000 m	(0.37, 0.44)		
Distance to	Pseudothreshold;	0.43	Pseudothreshold;	0.73		
Motorized Routes	30 m	(0.40, 0.47)	30 m	(0.68, 0.78)		
Elevation	Quadratic;	-0.62	Quadratic;	-1.14		
	30 m	(-0.65, -0.59);	1,000 m	(-1.19, -1.09);		
		0.87		0.34		
		(0.84, 0.90)		(0.31, 0.38)		
Hunter Effort	Linear;	-0.32	Pseudothreshold;	0.19		
	Hunting unit	(-0.35, -0.30)	Hunting unit	(0.16, 0.21)		
Slope	Quadratic;	0.70	Quadratic;	1.11		
•	1,000 m	(0.67, 0.72);	1,000 m	(1.07, 1.15);		
	,	-0.51	,	-1.06		
		(-0.55, -0.47)		(-1.11, -1.02)		
Snow Water	=	-	Linear;	-0.26		
Equivalent			1,000 m	(-0.30, -0.23)		
Solar Radiation	Quadratic;	0.55	Quadratic;	0.66		
	1,000 m	(0.53, 0.58);	1,000 m	(0.62, 0.71);		
	,	0.02	,	-0.34		
		(0.00, 0.05)		(-0.37, -0.30)		
Time Integrated	Pseudothreshold;	0.63	=	-		
NDVI	250 m	(0.61, 0.66)				
Canopy Cover *	-	1.28	-	0.39		
Access		(1.20, 1.36)		(0.34, 0.45)		
Distance to Route *	-	0.25	-	-0.46		
Access		(0.21, 0.30)		(-0.52, -0.39)		
Distance to Route *	-	-0.42	-	-0.29		
Canopy Cover		(-0.51, -0.32)		(-0.38, -0.20)		
Distance to Route *	-	0.95	-	1.15		
Hunter Effort		(0.91, 1.00)		(1.11, 1.19)		
Distance to Route *	-	-0.63	-	· -		
NDVI		(-0.69, -0.58)				
Distance to Route *	-	· -	-	-0.47		
SWE				(-0.50, -0.43)		

Notes: The second value presented for quadratic covariates represents the squared term.

Table 4. The estimated regression slope (and standard error) examining potential functional responses between the standardized coefficient estimates from the population specific models for hunter access, canopy cover, distance to motorized routes, and hunter effort along gradients of accessible:inaccessible and mean hunter effort for the population annual ranges. Values with confidence intervals that do not overlap 0 are bolded.

	Ar	chery	Rifle		
Covariate	Accessible: Inaccessible	Mean Hunter Effort	Accessible: Inaccessible	Mean Hunter Effort	
Hunter Access	1.23 (1.06)	0.02 (0.10)	-0.02 (1.03)	-0.10 (0.10)	
Canopy Cover	0.79 (0.82)	0.11 (0.07)	0.42 (1.00)	0.11 (0.10)	
Distance to Motorized Routes	1.06 (0.68)	0.19 (0.07)	0.81 (0.75)	0.20 (0.09)	
Hunter Effort	-1.09 (0.56)	-0.01 (0.08)	-0.06 (0.94)	0.06 (0.10)	

Table 5. The results of a comparison of the traditional security habitat paradigm based on ≥ 0.5 miles from a motorized route, ≥ 250 acre block size, and canopy cover varying from ≥ 0 - 70% in increments of 10% and secure area definitions based on results of the top ranked model and 6 different minimum block sizes (≥ 0 , 250, 500, 1,000, 2,000, and 5,000 km²) for each hunting season. During the archery season, the top model defined secure areas based on $\ge 13\%$ canopy cover (1,000 m spatial scale), ≥ 1.71 miles from a motorized route, and various block sizes. During the rifle season, the top model defined secure areas based on $\ge 9\%$ canopy cover (1,000 m spatial scale), ≥ 0.95 miles from a motorized route, and various block sizes.

MadalDaal	Archery		Rifle	
Model Rank	Model	ΔAIC_c	Model	ΔAIC_c
1	Archery $- \ge 0$ acres	0.0	Rifle - \geq 5,000 acres	0.0
2	Archery - ≥ 250 acres	88.9	Rifle $- \ge 0$ acres	24.7
3	Archery -≥ 500 acres	94.0	Rifle - \geq 500 acres	66.3
4	Archery - $\geq 1,000$ acres	138.2	Rifle - \geq 250 areas	90.4
5	Archery - \geq 2,000 acres	167.0	Rifle - \geq 1,000 acres	105.0
6	Archery - \geq 5,000 acres	229.7	Rifle - \geq 2,000 acres	151.6
7	Traditional - ≥ 10% Canopy	482.2	Traditional - \geq 0% Canopy	266.3
8	Traditional - \geq 0% Canopy	781.7	Traditional - $\geq 10\%$ Canopy	1327.1
9	Traditional - ≥ 20% Canopy	1088.0	Traditional - \geq 20% Canopy	1699.7
10	Traditional -≥30% Canopy	1208.4	Traditional - \geq 30% Canopy	1767.2
11	Traditional - ≥ 40% Canopy	1407.5	Traditional - ≥ 40% Canopy	1988.1
12	Traditional -≥50% Canopy	1843.8	Traditional - \geq 50% Canopy	2491.7
13	Traditional - ≥ 60% Canopy	2049.3	Traditional - \geq 70% Canopy	3214.8
14	Traditional - \geq 70% Canopy	2691.1	Traditional - ≥ 60% Canopy	3229.7

Figure 1. Distribution shifts in the 9 Montana elk populations that were included in this study. The x-axis represents 4 different time periods: summer (July and August), archery season, rifle season, and winter (Jan – March). The y-axis is the proportion of used points that are on publicly accessible lands. Populations are labeled as follows: BT = Blacktail, DM = Dome Mountain, EF = Bitterroot East Fork, MV = Madison Valley, PI = Pioneers, PV = Paradise Valley, SA = Sapphires, SC = Sage Creek, and WF = Bitterroot West Fork.

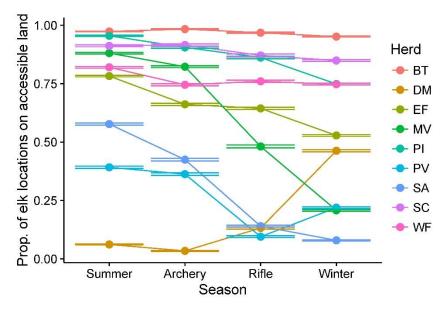


Figure 2. The study area included 9 elk population annual ranges in southwest Montana.

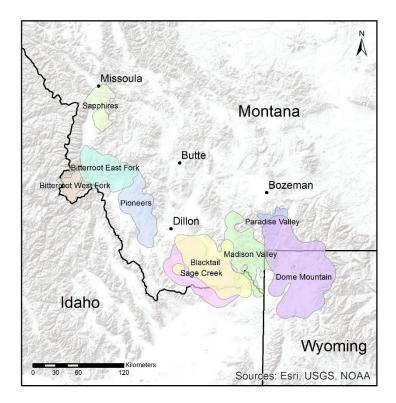


Figure 3. Plots of the main effects for the covariates included in the top archery season model, presented on the original, non-standardized scale. The plots present the coefficient estimate (line) and 95% confidence interval (shaded) for areas that allow or do not allow public hunter access across the available range for each covariate, with the other variables held at their mean value. The y-axis is analogous to the log-odds of selection.

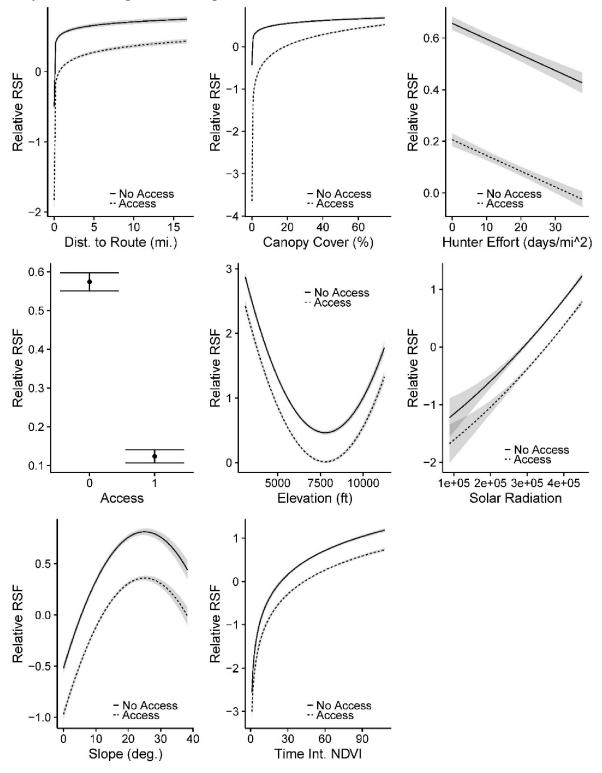


Figure 4. Plots of the interactions included in the top archery season model, presented on the original, non-standardized scale. Each row presents one interaction, with one of the interacting variables presented on the x-axis while the other is presented using two lines on the plot, one for a low value (1st quartile) and one for a high value (3rd quartile) of that covariate. The specific 'high' and 'low' values used are available in Appendix S4. The plots present the coefficient estimate (line) and 95% confidence interval (shaded) across the available range for each covariate, with the other variables held at their mean value. The y-axis is analogous to the logodds of selection.

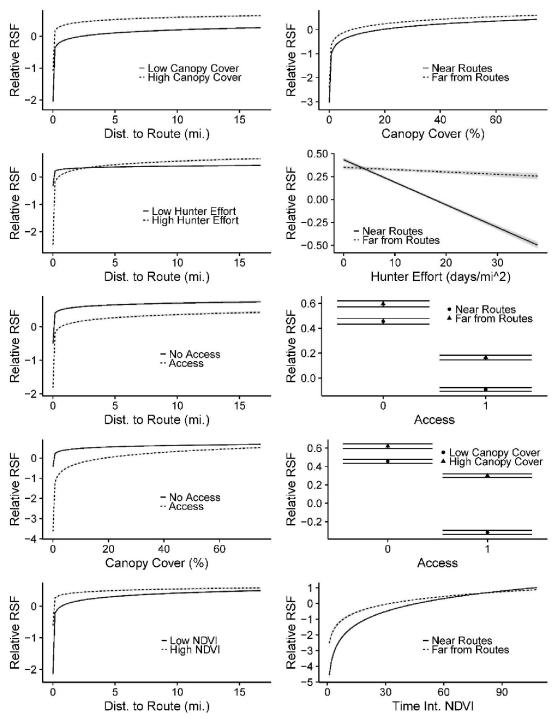


Figure 5. Plots of the main effects for the covariates included in the top rifle season model, presented on the original, non-standardized scale. The plots present the coefficient estimate (line) and 95% confidence interval (shaded) for areas that allow or do not allow public hunter access across the available range for each covariate, with the other variables held at their mean value. The y-axis is analogous to the log-odds of selection.

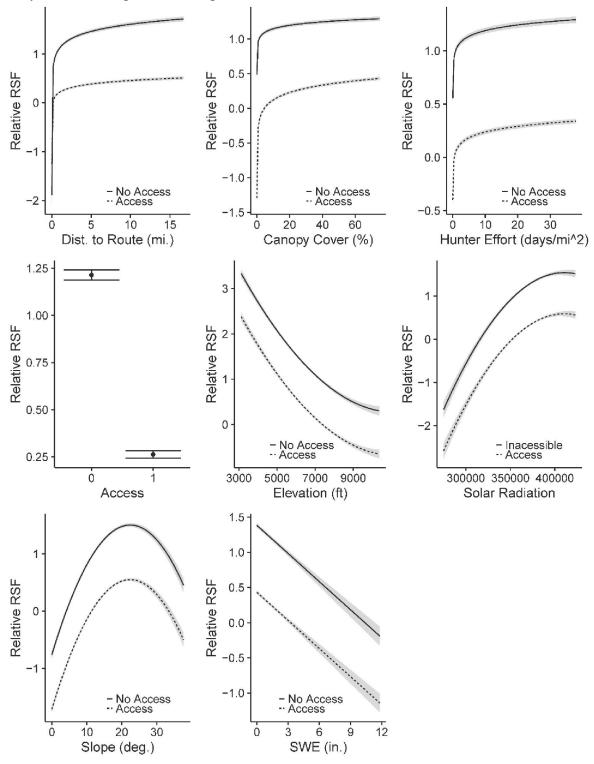


Figure 6. Plots of the interactions included in the top rifle season model, presented on the original, non-standardized scale. Each row presents one interaction, with one of the interacting variables presented on the x-axis while the other is presented using two lines on the plot, one for a low value (1st quartile) and one for a high value (3rd quartile) of that covariate. The specific 'high' and 'low' values used are available in Appendix S4. The plots present the coefficient estimate (line) and 95% confidence interval (shaded) across the available range for each covariate, with the other variables held at their mean value. The y-axis is analogous to the logodds of selection.

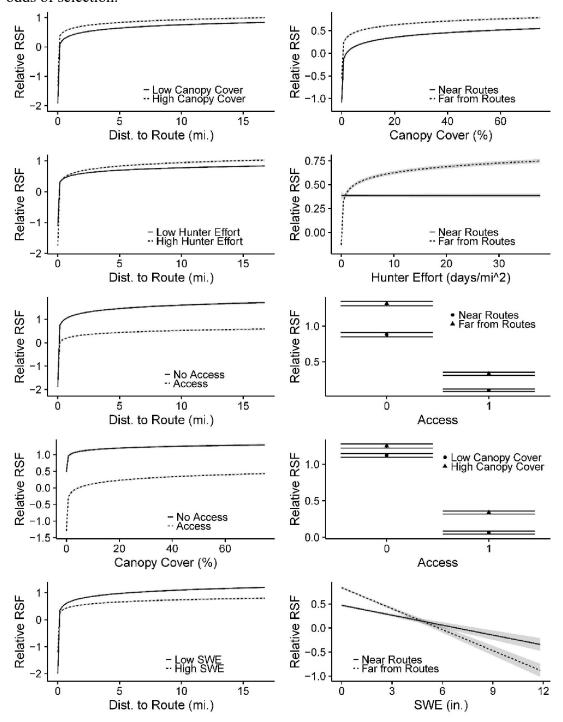


Figure 7. The relationship between the estimated effect of distance to motorized routes on the y-axis and mean hunter effort (days/km²) on the x-axis for the archery (Panel A) and rifle (Panel B) seasons. The standardized estimated coefficient from each population, and standard error, is presented with the results of the generalized least squares model designated by the dashed line. See Figure 1 for population abbreviations.

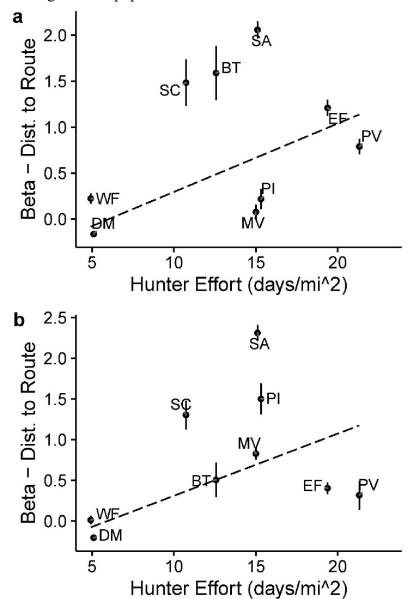
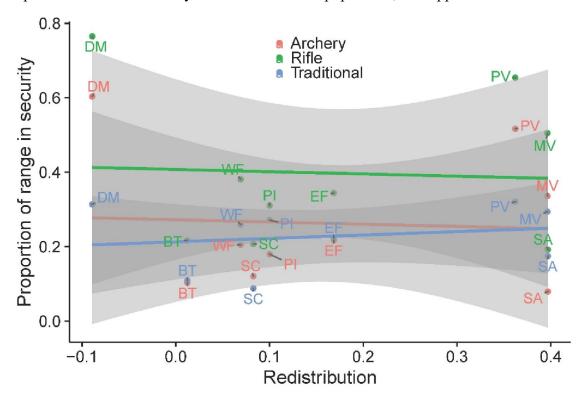


Figure 8. A comparison of the proportion of each population's annual range that is 'secure' based on the top archery (on \geq 13% canopy cover [1,000 m spatial scale], \geq 1.71 miles from a motorized route) and rifle (\geq 9% canopy cover [1,000 m spatial scale], \geq 0.95 miles from a motorized route, and \geq 5,000 acres) security area metrics and the traditional security area metric (\geq 40% canopy cover [30 m spatial scale], \geq 0.5 miles from a motorized route, and \geq 250 acres). These are based only the publicly accessible portion of each population's annual range. The amount of redistribution from publicly accessible to inaccessible lands for each population is also presented. Redistribution was defined as the change in proportion of locations on publicly accessible lands from August to rifle season. Population abbreviations same as Figure 1. For maps of the different security definitions for each population, see Appendix S5.



APPENDIX S1. The start and end dates for the archery and rifle hunting seasons for each of the years of the study, as defined by Montana Fish, Wildlife, and Parks harvest regulations.

Year	Arc	chery	Ri	Rifle		
rear	Start	End	Start	End		
2005	9/3/2005	10/16/2005	10/23/2005	11/27/2005		
2006	9/2/2006	10/15/2006	10/22/2006	11/26/2006		
2007	9/1/2007	10/14/2007	10/21/2007	11/25/2007		
2008	9/6/2008	10/19/2008	10/26/2008	11/30/2008		
2009	9/5/2009	10/18/2009	10/25/2009	11/29/2009		
2010	9/4/2010	10/17/2010	10/23/2010	11/28/2010		
2011	9/3/2011	10/16/2011	10/22/2011	11/27/2011		
2012	9/1/2012	10/14/2012	10/20/2012	11/25/2012		
2013	9/7/2013	10/20/2013	10/26/2013	12/1/2013		
2014	9/6/2014	10/19/2014	10/25/2014	11/30/2014		

APPENDIX S2. Covariate development and details

What follows is a breakdown of each covariate with details as to why they were selected, how they were generated, and the spatial scales and functional forms considered for each.

- Access access This covariate was used represent the differences in lands that are accessible to public hunters (public lands that permit hunting and private lands that are accessible to public hunters through a State hunter access program) and lands that are inaccessible to public hunters (public lands where hunting is not permitted and private lands with varying degrees of restrictions on public hunting access). This covariate was developed as a binary accessible/inaccessible (1/0) at the 30 x 30 m scale. Functional forms were not considered as this was a binary covariate.
- Canopy cover cc11 This layer was obtained from the National Landcover Database at 30 x 30 m resolution. Larger grain sizes represent a moving window average of percent canopy cover with the search window radius equal to the designated grain size. Canopy cover may have several different impacts on elk, as lower canopy covers may represent areas that provide feeding opportunities, while high cover may provide hiding cover (Lyon 1979, Johnson et al. 2000, Ager et al. 2003). This covariate was evaluated only for the pseudothreshold functional form.
- **Distance to open routes d2rd** This covariate was developed at 30 x 30 m resolution using the Euclidean Distance tool in ArcGIS 10.2. Only routes that were open to the public during the hunting seasons were used for this analysis (MFWP and USFS 2013). Distance to motorized routes is included as a covariate as it also represents the potential impact of roads on elk (Rowland et al. 2000, Ager et al. 2003). This covariate was only evaluated for the pseudothreshold functional form, as there is no reason to expect selection for/against an intermediate value. Larger spatial scales were not evaluated.
- Elevation elev Elevation is a key component of the physical landscape that has dramatic influences on water availability and vegetation and is often used in resource selection modeling. This layer was obtained at 30 x 30 m resolution. Larger spatial scales represent the moving window average elevation with a search radius equal to that of the designated spatial scale. This covariate was only evaluated for the quadratic functional form (Ranglack et al. 2014. In Review).
- **Hunter effort effort** An index of hunter effort was created for each hunt district. Total hunter effort was estimated for each hunt district as part of the Montana Fish, Wildlife and Parks harvest survey program, without respect to archery and rifle seasons. As the hunt districts are of varying size, effort was standardized for each hunt district by dividing by the area of the hunt district, resulting in an estimate of hunter days/km2. This was converted to a raster at 30 x 30 m resolution, but the values only varied by hunt district, thus larger spatial scales were not considered. This covariate varied annually.
- Slope slp Slope has various impacts on the landscape that can influence elk responses to different areas. Steep slopes may present barriers to travel and foraging, and may also be drier, impacting the vegetation types that are found there. There may also be differing risks of predation with slope, as mountain lions often hunt on steeper slopes that allow them to ambush their prey more easily (Logan and Irwin 1985, Husseman et al. 2003),

but steep slopes may offer protection from wolf predation (Laporte et al. 2010). Slope was generated at 30 x 30 m resolution based on the digital elevation model for the area using the Slope tool in ArcGIS 10.2. The larger spatial scales were calculated using a moving window average with a search radius equal to that of the spatial scale. The resulting rasters contained extremely small values, thus they were multiplied by 1000 to allow for easy extraction in integer form. This covariate was only evaluated for the quadratic functional form (Ranglack et al. 2014. In Review).

Snow Water Equivalent – swe - Snow accumulation is strongly associated with the ecology and behavior of animals in cold climates, as snow can reduce access to forage patches (Craighead et al. 1973, Bruggeman 2006) and increase energy expenditure for thermoregulation, travel, and search for food (Parker et al. 1984, Telfer and Kelsall 1984). We used snow water equivalent (SWE) data from the Snow Data Assimilation System (SNODAS) Data Products at the National Snow and Ice Data Center (http://nsidc.org/data/docs/noaa/g02158_snodas_snow_cover_model/). As now accumulations are unlikely to impact elk resource selection during the earlier archery season, SWE was only included for the rifle analysis. We generated SWE rasters based on the max SWE value for each pixel during each of six 6-day periods during the rifle season which we called 'hunt period'. These hunt periods were unique for each year. As the data is only available at the 1,000 m scale, no other spatial scales were evaluated. Both the linear and pseudothreshold functional forms were evaluated. This covariate varied every 6 days during the annual rifle seasons.

Solar radiation – sr – Solar radiation in this study is used as a surrogate for aspect. The amount of solar radiation received by an area can impact the water balance and thus the vegetation types that are found in the area (Fu and Rich 2002). This was generated at 30 x 30 m using the Area Solar Radiation tool in ArGIS 10.2. Inputs were the elevation DEM and the time frame of July 1 – August 31, 2009, as that represented the desired months of the year and roughly the mid-point of the study. All other options were set to their defaults. The larger spatial scales were calculated using a moving window average with a search radius equal to that of the spatial scale. The resulting rasters contained extremely large values, thus they were divided by 1000 to allow for extraction. This covariate was only evaluated for the quadratic functional form (Ranglack et al. 2014. In Review).

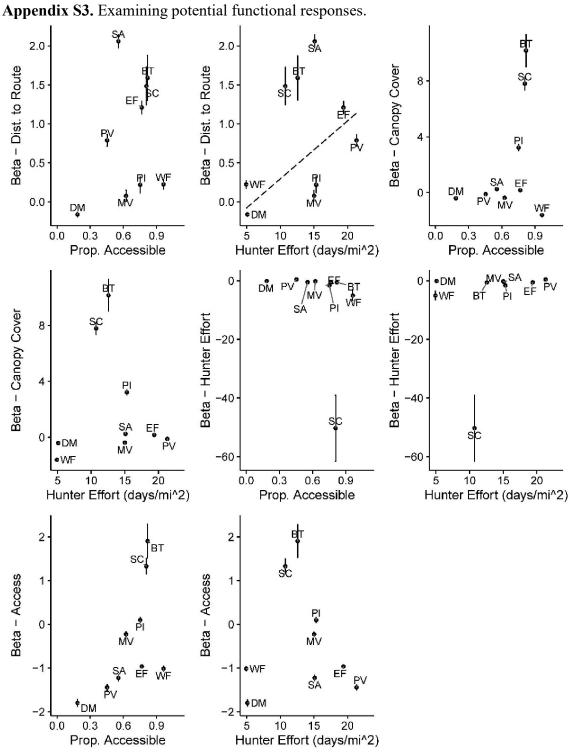
Time Integrated NDVI – tin – Time-integrated NDVI is the daily (interpolated) integration of NDVI values above the start of season NDVI baseline for the entirety of the growing season. It therefore represents the net primarily production during the growing season for each pixel (Jonsson and Eklundh 2002, White et al. 2009). As such, the influence of forest canopy on forage available to ungulates (Borowik et al. 2013) is mediated, as the value is simply the entire area under the NDVI curve from the start of the growing season to the end. This was downloaded for each year in a pre-processed format from http://phenology.cr.usgs.gov/get_data_250w.php at 250 m resolution, with the larger spatial scales calculated using a moving window average with a search radius equal to that of the spatial scale. This covariate was only evaluated for the pseudothreshold functional form during the archer season (Ranglack et al. 2014. In Review). This covariate varied annually.

Traditional paradigm – hillis – The Hillis paradigm (Hillis et al. 1991) is often used for defining security areas for elk, and is a combination of distance to routes ≥0.5 miles, and size of the security block (≥250 acres). We tested several different levels of minimum canopy cover (≥0, 10, 20, 30, 40, 50, 60, 70%). The raster was generated at 30 x 30 m resolution as a binary secure/unsecure (1/0). This covariate was only considered in a post-hoc comparison of the traditional paradigm versus new paradigms of security habitat based on our top model results.

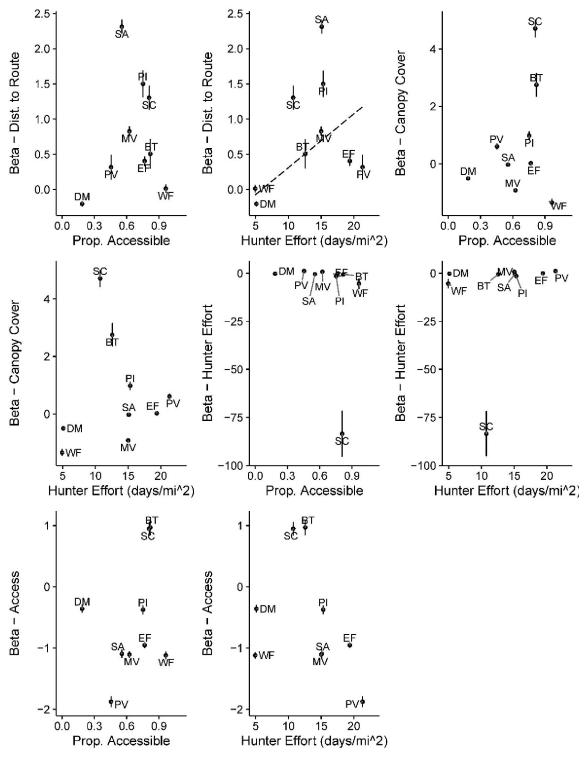
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Examining the potential for a functional response between the estimated effect of distance to motorized routes, canopy cover, hunter access, and hunter effort on the y-axis and proportion of annual range that is publicly accessible and mean hunter effort (days/km²) on the x-axis for the archery season. The points represent the standardized coefficient estimate from each population, along with the associated standard error. Any significant ($p \le 0.05$) relationships are represented by a dashed line. See Figure 1 for population abbreviations.



Examining the potential for a functional response between the estimated effect of distance to motorized routes, canopy cover, hunter access, and hunter effort on the y-axis and proportion of annual range that is publicly accessible and mean hunter effort (days/km²) on the x-axis for the rifle season. The points represent the standardized coefficient estimate from each population, along with the associated standard error. Any significant ($p \le 0.05$) relationships are represented by a dashed line. See Figure 1 for population abbreviations.

Appendix S4. 'Low' and 'high' values used in Figures 4 and 6, which correspond to the 1st and 3rd quantiles from the pooled data, presented for both the archery and rifle seasons.

Covariate	Archery		Rifle	
	Low	High	Low	High
Distance to motorized route	0.32	2.20	0.32	2.09
(miles)	7.85	41.66	6.87	40.67
Canopy Cover (%) Hunter Effort (hunter	7.83 7.61	20.0	7.61	20.7
days/mile ²)	7.01	20.0	7.01	20.7
Time Integrated NDVI	42	60	-	-
SWE (in.)	-	-	0.20	1.93

Appendix S5. Maps comparing the traditional security areas with the top security area metrics from the top archery and rifle season models for each population used in the analysis. Traditional security areas are defined as areas of at least 250 acres, that have at least 40% canopy cover (30 m scale), and are at least 0.5 miles from the nearest motorized route. Archery security areas have at least 13% canopy cover (1,000 m scale) and are at least 1.71 miles from the nearest motorized route, with no block size requirement. Rifle security areas are defined as areas of at least 5,000 acres, that have at least 9% canopy cover (1,000 m scale), and are at least 0.95 miles from the nearest motorized route. Security areas based on all of the definitions are shown in blue, with each row representing one population and each column representing a different security definition. Population annual ranges are designated by the black line, as defined by a 99% KDE.

